

# The distribution of ant nests (Hymenoptera, Formicidae) in coastal grey dunes of Flanders (Belgium) and their relationship to myrmecochorous plants

Valérie Lehouck<sup>1</sup>, Dries Bonte<sup>1</sup>, Wouter Dekoninck<sup>1</sup> and Jean-Pierre Maelfait<sup>1,2</sup>

<sup>1</sup> University of Ghent, Research Group Terrestrial Ecology, Ledeganckstraat 35, B-9000 Ghent, Belgium

<sup>2</sup> Institute of Nature Conservation, Kliniekstraat 25, B-1070 Brussels, Belgium

Corresponding author : V. Lehouck, e-mail : [v-lehouck@tiscalinet.be](mailto:v-lehouck@tiscalinet.be)

**ABSTRACT.** During the summer of 2001, we conducted a study on the spatial distribution of ants in coastal grey dunes (Oostduinkerke, Western Flanders, Belgium). Nest locations of the most abundant ant species were analysed with multivariate techniques. *Tetramorium caespitum* frequented moss-dominated vegetation, whereas *Myrmica sabuleti*, *M. scabrinodis*, *Lasius flavus* and *L. meridionalis* preferred grassy vegetations. *Formica cunicularia* and *L. psammophilus* occurred in all types of grey dune vegetation. According to recent literature, a positive spatial relationship can exist between the positioning of ant nests and the location of the myrmecochorous plants *Viola curtisii*, *Luzula campestris* and *Polygala vulgaris* in coastal dunes. Neither preliminary investigations, nor our study could confirm this significant positive relationship : the occurrence of myrmecochorous plants seems to be independent of the proximity of nests. It is possible that relationships are masked by a high turnover rate of the nest sites or by a restricted seedling establishment. We did not, however, observe ants transporting seeds of *Viola*, *Luzula* or *Polygala* in the field, possibly indicating the inefficiency of searching for those seeds in areas where population densities of these plants are rather low and other food sources are abundantly available.

**KEY WORDS :** myrmecochory, *Polygala vulgaris*, *Luzula campestris*, *Viola curtisii*.

## INTRODUCTION

Habitat characteristics are relatively well studied for most ant species in Western Europe (cf. SEIFERT, 1996), but few more detailed characterisations of nest location are available (DEKONINCK & BONTE, 2002). However, the relationship with myrmecochores is unclear and not unambiguously documented. Myrmecochores are plants from which diaspores are transported by ants (SERANDER, 1906). Most of them have a specialized structure, the elaiosome, containing a lot of fatty acids and providing up to one third of the total energy amount (LISCI et al., 1996). Several hypotheses have been put forward to explain the possible advantages of myrmecochory : escape from seed predation (CULVER & BEATTIE, 1978; O'DOWD & HAY, 1980; HANZAWA et al., 1985; OHARA & HIGASHI, 1987), avoidance of competition with congeneric species (HANDEL, 1978; HIGASHI et al., 1989; OKHAWARA et al., 1996) and relocation of the seeds to favourable (nutrient-enriched) sites for germination and establishment (CULVER & BEATTIE, 1978, 1980 and 1983; DAVIDSON & MORTON, 1981; GREEN et al., 1998). RICE & WESTOBY (1986) and BOND & STOCK (1989), on the other hand, found that seed transport by ants in sclerophyll vegetation does not always result in deposition at nutrient enriched sites. Apparently, advantages for the plants of the transport of myrmecochore seeds by ants are not universal. It seems that the results are strongly dependent on the habitat type and the ant species involved.

Most studies of myrmecochory have been carried out in a variety of biotope types, such as temperate forests

(OKHAWARA et al., 1996; GORB & GORB, 1998), mountain meadows (CULVER & BEATTIE, 1983; KOVÁR et al., 2001), sclerophyll vegetation (RICE & WESTOBY, 1986; BOND & STOCK, 1989) and deserts (O'DOWD & HAY, 1980). However, information about myrmecochory in coastal dunes is still scarce. According to LACK & KAY (1987), OOSTERMEIJER (1989) and KOVÁR et al. (2001), a spatial relationship with these myrmecochores can be expected, since ants transport their seeds in laboratory experiments (SERANDER, 1906). KOVÁR et al. (2001) found that myrmecochores had a non-random distribution in mountain grasslands, growing mainly on the edge of nests of *Lasius flavus*, *Tetramorium caespitum* and *Formica* spp. We wanted to compare the results of the study of OOSTERMEIJER (1989) in the dunes of Terschelling (the Netherlands) with the situation in Oostduinkerke (Belgium). OOSTERMEIJER (1989) demonstrated with mapping studies that the dispersal of seeds by ants has a marked effect on the distribution pattern of the standing population of *Polygala vulgaris* and *Viola curtisii*. Adult plants were found on or close to the active nest mounds of all ant species present, while growing sites of juvenile plants and seedlings were practically restricted to the nest environments. DEKONINCK & BONTE (2002), however, did not detect a positive spatial relationship during a preliminary study in the Oostvoorduin, part of our study site, for the same plant species and mainly the same ant species.

In this contribution, we characterised nest location in relation to the vegetation structure and the presence and abundance of the myrmecochores *Polygala vulgaris*, *Viola curtisii* and *Luzula campestris*. Our aim was not to

work out whether there is a causal relationship between the distribution of both ants and plants, but to describe possible spatial effects.

A perusal of the relevant literature reveals that all of the ant species in our study area show seed-carrying behaviour (SERANDER, 1906; CULVER & BEATTIE, 1980 and 1983; OOSTERMEIJER, 1989).

## MATERIAL AND METHODS

### Study site

The research took place in the coastal dunes of Ter Yde (Oostduinkerke, West-Flanders, Belgium, Fig. 1), at three sites sharing a common geological history : 62.3 ha (with cattle grazing only in the non-studied part), 76.4 ha (with 16 sheep and 4 ponies) and 47.6 ha (3 ponies). Grey dunes and dense grasslands on lime-rich soils dominate the vegetation.

Coastal 'grey dune' is most readily defined using plant communities. Vegetation includes moss-dominated dunes as well as dune grassland (with a distinct organic soil layer) belonging to the *Cladonio-Koelerietalia* (PROVOOST et al., 2002). On the moss dunes, species such as *Tortula ruralis* or, in more fixed conditions, *Hypnum cupressiforme*, are dominant and accompanied by therophytes (*Crepis capillaris*, *Leontodon saxatilis*, ...). In the

grasslands, we find species such as *Asperula cynanchica*, *Potentilla erecta*, *Thymus pulegioides*, *Galium verum*, *Festuca rubra* and often a lot of *Avenula pubescens*.

### Nest location as a function of vegetation structure and myrmecochores

During the summer of 2001, 59 plots ( $3 \times 3 \text{ m}^2$  – quadrats) were placed around a randomly chosen ant nest. These plots were divided into nine quadrats of  $1 \times 1 \text{ m}^2$  (Fig. 2). This was done to check whether ants are restricted to a certain vegetation composition on both larger and smaller scales, and if so, whether there is a difference in their response towards both scales. For the relationship with myrmecochores, a look at these two scales seemed interesting to us because it is a simplified measure for the distance ant nest to plant; in each quadrat we can determine the presence and the amount of myrmecochores in relation to the presence or abundance of a certain ant species and the other way around. Since foraging range differs among ant species but usually does not exceed 1 m (GOMÉZ & ESPADALER 1998b), we chose  $1 \times 1 \text{ m}^2$  quadrats as our smallest space unit. We expect a spatial relationship to be found on a small scale (myrmecochores in direct vicinity of ant nests) but perhaps not on a larger scale (see OOSTERMEIJER (1989), who found all plants concentrated in a 20 cm-range of the nest). For each of the plots and quadrats, we assessed the coverage



Fig. 1. – Study site. The shaded area indicates the zones studied.

of mosses, bare soil, shrubs and grasses and herbs (in%). For the herb-layer, three categories were used according to the vegetation-height (VLV=very low vegetation (1-3 cm), LV=low vegetation (3-20 cm), HV=high vegetation (> 20 cm)). We dug at about 20 (but up to 60, depending on population densities) random points per 3 x 3 m<sup>2</sup>-quadrat. We sampled a 15 x 15 cm surface area to a depth of about 30 cm (most calices from *Lasius psammophilus* are at a depth of 10-30 cm, see SEIFERT 1996). Sampling places where more than ten workers occurred (see also SERRANO et al., 1993) or where males or larvae were found were mapped. One colony is spatially defined as the group of all contiguous spatial sampling places with presence of the same species (see also SERRANO et al., 1993). The percentage of undermined soil was then estimated on these maps using the surface area of the 'colonies'. This was necessary because it appeared impossible to discriminate between adjoining nests in *Tetramorium caespitum* and *L. psammophilus*, presumably because of calices leading to subterranean food resources (e.g. aphid-colonies).

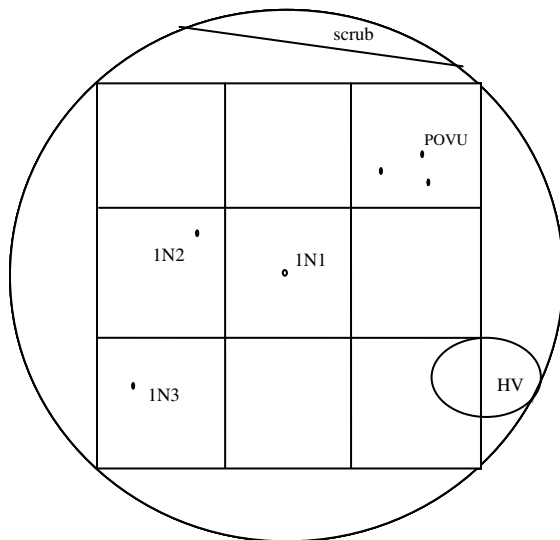


Fig. 2. – Study plot with indication of ant nests (1N1, 1N2 and 1N3), vegetation structures (Scrub; HV=high vegetation) and myrmecochores (here: POVU=*Polygala vulgaris*). A small quadrat measures 1 x 1 m<sup>2</sup>.

For each nest-unit, a sample of at least three workers was collected and identified using SEIFERT (1988a, 1988b, 1996 and 1997). The coverage of the myrmecochores *Luzula campestris*, *Polygala vulgaris* and *Viola curtisii* was also estimated and individual plants were indicated on the map (individuals could not be discerned for *L. campestris* because of its patchy distribution patterns caused by its clonal growth).

### Data analysis

Multivariate analyses (DCA) were carried out with PC-ORD (version 4.20, MC CUNE & MEFFORD, 1997) to reveal overall trends in the ant data sets. The purpose here was to classify plots based on vegetation structure data, so that further analysis to examine the relationship between ants and myrmecochores could be performed, taking into account habitat preferences of both ant and plant species. Data on percentage of undermined soil per

ant species and per plot were first put into perspective by dividing this percentage by the total percentage of undermined soil for each species (in all plots together). The data were Arcsin-transformed before performing the DCA, as is recommended for data expressed as a percentage (SOKAL & ROLPH, 1981). Pearson-correlation of the plot scores with vegetation structure data was used to explain the biological meaning of the axes. Pearson-correlations (SOKAL & ROLPH, 1981) were also used to test co-correlation between vegetation structure and the abundance of myrmecochores.

Univariate tests were performed using the statistical program STATISTICA (version 6.0, STATSOFT, 1994) with a significance level taken at 0.05. A Mann-Whitney-U-test was used to check the existence of a possible relationship between the abundance of certain ant species and the presence of the myrmecochorous plant species. Chi<sup>2</sup>-tests (SIEGEL, 1956) were performed to analyse absence/presence trends between myrmecochores and ant species. Bonferroni corrections were used in case of multiple comparisons.

## RESULTS

### General results

Twelve species were found in the study area, with *Lasius psammophilus* the most abundant species, followed by *Tetramorium caespitum*, *Formica cunicularia* and *Myrmica sabuleti* (Table 1). The social parasite *Lasius meridionalis* was also well represented (27.8% of the nests of *Lasius psammophilus*, the host species, were 'infected' by *L. meridionalis*).

TABLE 1

List of species and their frequency in the study area.

Species	# plots of 59 (%)
<i>Formica cunicularia</i> Latreille 1798	18 (30.5)
<i>Lasius psammophilus</i> Seifert 1992	36 (61.0)
<i>Lasius niger</i> (Linnaeus 1758)	7 (11.9)
<i>Lasius fuliginosus</i> (Latreille 1798)	1 (1.7)
<i>Lasius meridionalis</i> (Bondroit 1919)	10 (16.9)
<i>Lasius flavus</i> (Fabricius 1781)	7 (11.9)
<i>Myrmica sabuleti</i> Meinert 1860	16 (27.1)
<i>Myrmica scabrinodis</i> Nylander 1846	5 (8.5)
<i>Myrmica specioidea</i> Bondroit 1918	4 (6.8)
<i>Myrmica rugulosa</i> Nylander 1846	1 (1.7)
<i>Myrmica rubra</i> (Linnaeus 1758)	1 (1.7)
<i>Tetramorium caespitum</i> (Linnaeus 1758)	26 (44.1)

### Nest location in relation to vegetation structure

DCA-ordination revealed three relevant axes, explaining variation in nest-location of ants as a function of the vegetation structure. The percentage of variance explained by these factors was rather low (17.4%, 16.2% and 10.5% for axis 1, 2 and 3 respectively), indicating a quite high variance in the samples. Still, trends can be observed in the results of the DCA (Fig. 3).

However, no linear relations with the first axis were found (Table 2). Along this axis, one 3 x 3 m<sup>2</sup>-quadrat, in which *L. niger* was abundantly present, was separated from

the rest. *L. psammophilus* was the only accompanying species in this plot, not exceeding an undermined soil surface of 1%. The ant species composition in this plot was thus very different from the others. The second axis was significantly positively correlated with the moss coverage and negatively with the herb layer and the abundance of *Polygala vulgaris* (but there was a strong positive correlation between the abundance of POVU and LV, see further). The third axis was only significantly negatively correlated with the estimated ground coverage of *Polygala vulgaris* (Table 2). Correlations with vegetation cover characteristics along this axis were not significant after Bonferroni-correction, but indicate biologically relevant relations.

*Tetramorium caespitum* was found in plots with a lot of mosses, in contrast to *Myrmica sabuleti* and *M. scabrinodis*, which were found in grassy vegetation. *Lasius flavus* and *L. meridionalis* also seemed to prefer grasslands, but they differed from the *Myrmica*-species, which were found in plots with higher vegetation and without *Polygala vulgaris*. *M. specioides* seems to prefer a habitat with a lot of mosses, but was sometimes found in grasslands as well. Nests of *L. niger* were often found in disturbed patches, both with mosses and herbs/grasses. *Formica cunicularia* and *L. psammophilus* showed no clear preference for any grey dune vegetation structure (Fig. 3).

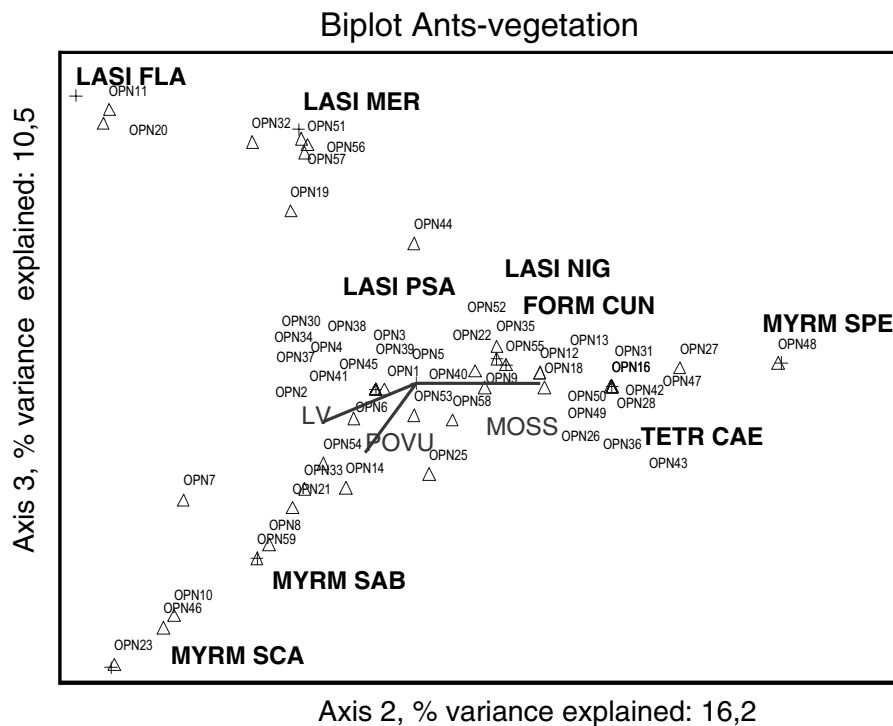


Fig. 3. – DCA-biplot ant nest location as a function of the vegetation structure. Species that were found in only one plot were omitted. Triangles indicate the plot number ('opn' 1-59), + - symbols indicate ant species. Components :  $\lambda_1=0.99$ ,  $\lambda_2=0.92$ ,  $\lambda_3=0.60$ . Total inertia : 5.70. Legend : MOS=mosses; LV=low vegetation (mainly herbs, up to 20 cm); POVU=*Polygala vulgaris*; MYRM SCA=*Myrmica scabrinodis*; MYRM SAB=*Myrmica sabuleti*; MYRM SPE=*Myrmica specioides*; TETR CAE=*Tetramorium caespitum*; FORM CUN=*Formica cunicularia*; LASI NIG=*Lasius niger*; LASI PSA=*Lasius psammophilus*; LASI MER=*Lasius meridionalis*; LASI FLA=*Lasius flavus*.

TABLE 2

Pearson-correlation-coefficients between the ordination scores (Fig. 3) and the estimated vegetation coverage and coverage of the myrmecochores *Viola curtisii* (VICU), *Luzula campestris* (LUCA) and *Polygala vulgaris* (POVU). Abbreviations : HV=high vegetation (> 20 cm); LV=low vegetation (3-20 cm); VLV= very low vegetation (< 3 cm); MOSS=mosses; SAND=bare soil; SHRUB=shrub; total cover=HV + LV + VLV + SCRUB + MOSS; herb layer=HV + LV + VLV. Bold :  $p < 0.0045$  (significant after Bonferroni-correction). \* :  $p < 0.05$  (NS after Bonferroni-correction).

	HV	LV	MOSS	SHRUB	VLV	SAND	Total cover	Herb layer	VICU	LUCA	POVU
Axis 1	0.2053	-0.0059	-0.151	0.268*	-0.045	-0.058	0.058	0.142	-0.038	0.146	-0.053
Axis 2	-0.2835*	<b>-0.515</b>	<b>0.592</b>	0.014	0.260	0.100	-0.100	-0.580	.174	-0.227	<b>-0.388</b>
Axis 3	0.3145*	-0.332*	0.0093	-0.0234	-0.003	0.076	-0.077	-0.028	0.1315	-0.060	<b>-0.443</b>



*T. caespitum* and *L. psammophilus*, the two most abundant species, were rarely found together in the same plot ( $\chi^2=11.21$ ,  $p < 0.001$ ), except in grass-plots (in three of the four cases where *T. caespitum* was present, *L. psammophilus* was also found ( $\chi^2$ ,  $p > 0.05$ )).

### Nest location in relation to the distribution of myrmecochores

The finding that the presence or the abundance of *Polygala vulgaris* could be an important factor determining ant nest location (or the other way around : ants determine plant distribution) has to be interpreted with caution since the myrmecochores studied each have their own habitat preferences as well. In Figure 3, one can see that *M. sabuleti* and *M. scabrinodis* are indicative for low-vegetation grasslands, often in the presence of *Polygala vulgaris*, whereas *L. flavus* and *L. meridionalis* are found in grasslands with a higher vegetation and without this plant species.

*Polygala vulgaris* was only present in short grazed grasslands and there was a strong positive correlation between the cover-percentage of this myrmecochore and the percentage of low vegetation ( $R=+ 0.36$ ,  $p < 0.001$ ). The same is true for *Viola curtisii* and the coverage of bare soil ( $R=+ 0.38$ ,  $p < 0.001$ ) and for *Luzula campestris* and the low and higher herb layer (respectively  $R=+ 0.64$  and  $R=+ 0.45$ ; both  $p < 0.001$ ). In the case of *Polygala vulgaris* and *Luzula campestris*, there is also a significant negative correlation with the moss-coverage (respectively  $R=-0.45$ ;  $R=-0.63$ ; both  $p < 0.01$ ).

On the largest scale ( $3 \times 3 \text{ m}^2$ ), a significant positive association was found between the presence of *L. psammophilus* ( $\chi^2$ -test,  $p=0.025$ ) and *M. sabuleti* respectively ( $\chi^2$ -test,  $p=0.047$ ) with the presence of *L. campestris* in moss dunes but this association was lacking in grassland vegetation. This result again suggests that vegetation structure is more important than the presence of myrmecochores per se. At a scale of  $2 \times 2 \text{ m}^2$  and  $1 \times 1 \text{ m}^2$ , the relationships were no longer significant, except for all plots together (both grassland and moss dunes). *Myrmica scabrinodis* showed a marginally significant positive association in its presence with the presence of *Polygala vulgaris* ( $\chi^2$ -test,  $p=0.047$ ). For the other ant and plant species, there was no significant relationship at any spatial scale in terms of presence/absence at different scales.

Besides a lack of significant association in terms of presence/absence between ant species and myrmecochores, the abundance of several ant species per plot (measured by the percentage of nest cover) was also not significantly influenced by the presence of myrmecochores (Mann-Whitney-U-tests,  $p > 0.05$ ).

## DISCUSSION

### Nest location in relation to vegetation structure

According to the DCA ordination, species have distinctive habitat preferences, even within grey dunes. The vegetation structure (coverage, height) is an important factor determining the habitat of several species, as was earlier mentioned by BOOMSMA & VAN LOON (1982), HANDELMANN (1997); BLOMQUIST et al. (2000); LOPÉZ et al.

(2000) and DEKONINCK & BONTE (2002). Our results on habitat preferences are in agreement with the literature (ASSING, 1986; VAN BOVEN & MABELIS, 1986; SEIFERT, 1996; BOER & DE GRUYTER, 1999; BOER, 2001 and DEKONINCK & BONTE, 2002).

We believe that *T. caespitum* is an even earlier pioneer than *L. psammophilus*, as both were rarely found together in the same plot, which could be an indication of habitat segregation because of interspecific competition, with *T. caespitum* being the first pioneer established in dry moss dune vegetation, followed by the colonisation of the more fixed habitat by *L. psammophilus*. This confirms the findings of BOOMSMA et al. (1987) who noted the presence of *T. caespitum* on all 17 of the Frisian Islands, while *L. psammophilus* was only found on Texel, the biggest island, near the mainland, indicating *T. caespitum* is a more mobile species or a better survivor.

### Nest location in relation to the distribution of myrmecochores

Our analyses do not indicate the existence of a relationship between ant nest location of any ant species and the presence of myrmecochores. The association between the myrmecochore *P. vulgaris* and *M. scabrinodis* is probably the result of co-variation with vegetation structure and can neither be rejected nor confirmed.

OOSTERMEIJER (1989) documents a significant relationship between the location of the myrmecochores *V. curtisii*, *L. campestris* and *P. vulgaris* on the one hand, and the position of ant nests of *L. niger*, *T. caespitum*, *F. fusca*, *F. rufibarbis* and *M. schencki* on the other hand. In Terschelling, this author found most of the myrmecochorous plants on or in the close proximity (20 cm) of the nests, independently of the ant species involved. Our results do not confirm this. Earlier, DEKONINCK & BONTE (2002) also did not find a positional ant-plant relationship in the Oostvoorduin, as was the case in our study. They worked with the same species as the ones found in our study area. The spatial relationship between ants and myrmecochores can be two-sided :

Firstly, the spatial distribution of ant nests could be influenced by the presence and the amount of myrmecochores (the availability of the nutritious seeds). In this case, one would expect ant nests to be more abundant in the proximity of myrmecochores, which was not the case in our study. Vegetation structure seemed much more important in determining the presence of certain ant species than the presence of myrmecochores. We suppose that ants search for their food along trial ways, and take all the food they meet on their path (see also MULL & MACMAHON, 1997). Since population density of the myrmecochores studied was rather low in our study site, we think ants take seeds that are abundantly available (e.g. *Phleum arenarium* grass-seeds) instead of searching for seeds of these myrmecochores. We suggest that the availability of the seeds is an important factor because ants took myrmecochorous seeds under laboratory conditions (LEHOUCK et al., unpubl.), which shows that seed carrying by all ant species in our study area is possible, as mentioned in literature (e.g. SERNANDER, 1906). CULVER & BEATTIE (1978) state that the chance to encounter ant-dispersed plant species could make a 'behavioural' differ-

ence, in that dispersion is much less efficient in areas where ant-dispersed plant species are rather scarce. Although LACK & KAY (1987) supposed the existence of a possible search image, this has never been confirmed, but availability may play an important role here as well. In our study area there was enough food to provide ant colonies with the energy needed: insects, non-myrmecochorous seeds, honeydew, nectar, ... and most ants are not strictly granivorous, nectivorous or insectivorous. They have a combined diet (ALONSO, 2000). It is possible that the presence of myrmecochores determines ant nest distribution in areas with a dense population of myrmecochores (as was the case in the study of OOSTERMEIJER (1989), who performed his study in a moist dune valley) or low food availability. According to KJELLSSON (1985), dispersion-efficiency of myrmecochorous seeds clearly depends on the acute requirement for food in an ant colony, as well as the distance of the food source to the nest.

Secondly, the location of the myrmecochorous plants could be determined by seed transport by ants. As a consequence, one should expect plants to grow in the close proximity of ant nests. In our study, this was not the case. Data were analysed on several spatial scales and significant trends at the largest scale ( $3 \times 3 \text{ m}^2$ ) were often not significant at smaller scales ( $2 \times 2 \text{ m}^2$ ,  $1 \times 1 \text{ m}^2$ ). Several authors mention the concentration of myrmecochorous plants on ant nests (SERANDER, 1906; DAVIDSON & MORTON, 1981; OOSTERMEIJER, 1989), while others find them on the edge of the nests (KJELLSSON, 1985; OOSTERMEIJER, 1989; GOMÉZ & ESPADALER, 1998a; GORB & GORB, 1998; KOVÁR et al., 2001). This suggests that elaiosomes are removed, while seeds can germinate in 'refuse piles'. Even if the whole seed is initially taken into the nest, it is possible that the seed with the discarded elaiosome is removed afterwards (LACK & KAY, 1987). CULVER & BEATTIE (1983) even found a negative relationship between the position of myrmecochorous plants and ant nests of *Formica canadensis* in a mountain meadow in Colorado, USA (no plants on ant nests). They thought that establishment of seedlings could be restricted chemically (see also SEIFERT 1996) or mechanically. Pathogenic infection is also thought to be increased (CHRISTENSEN, 1972 in: KJELLSSON, 1985). Since OOSTERMEIJER (1989) did find seedlings on nests in coastal dunes, one could say that these arguments are probably not valid in our case (i.e. with these particular plant and ant species, both in Terschelling and Oostduinkerke). However, there are some 'small', but important, differences between the two study areas. In our study area, there have been no rabbits for the last ten years, because of a serious epidemic of myxomatosis. Seed predation by rabbits is therefore not applicable in our study site. Seed burial by ants protects the seeds against predation (e.g. O'DOWD & HAY 1980). Since rabbit grazing is intensive in Terschelling (pre-dispersal predation of 70% of the seeds of *Viola* and *Luzula*), it is possible that seeds germinate in ant nests but not in the surroundings in the study area of OOSTERMEIJER (1989), whereas germination is possible everywhere in our study site. The absence of rabbits in our study would mean that germination of myrmecochores is not restricted by predation by rabbits, nor in the nests, nor in the surroundings. This could explain the absence of any positive relationship in our study. Next, a behavioural difference

in seed transport by ants of the same species in different studies could be more apparent than real. Habitat is likely to play an important role in the outcome (CULVER & BEATTIE, 1978). The slight habitat differences between the study of OOSTERMEIJER (1989) and our study (moist dune valley versus grey dunes) could make differences in ant behaviour and germination chances through differences in soil conditions and infection rate by pathogens. The first can explain why ants do not choose to make their nests in close proximity to myrmecochorous plants, whereas the latter could be an explanation for the fact that myrmecochores were not found on/in the vicinity of ant nests in our study. It is strange, however, that OOSTERMEIJER (1989) found nest translocation to be infrequent (no translocation observed within five years). According to CULVER & BEATTIE (1978), the fact that ants frequently abandon their nests may be crucial for the germination of the seeds. They found that seed scarification was an opportunity for germination but if seeds, especially during germination, are subject to a continuing disturbance by ants – excavating more tunnels or gnawing new shoots – this advantage is likely to be lost. Certain authors mention a high turn over rate of nests. CULVER & BEATTIE (1978) found that 15 out of 23 nests of *Aphaenogaster* sp. moved within 11 days; *L. niger* is known to shift nest sites regularly (SMALLWOOD & CULVER, 1979). This nest site translocation could cause the absence of a spatial relationship, especially when considering adult plants instead of seedlings: movement of the nests is then faster than the time between the collection of the seeds and seedling emergence. Moreover, all three myrmecochores studied are perennials (*P. vulgaris* can reach an age of 5–10 years (LACK & KAY, 1987)). DEKONINCK & BONTE (2002) thought nest site translocation could explain the absence of a spatial relationship in the Oostvoorduin. In the area they studied, turnover rate of nest sites is high, probably because of disturbance by intensive cattle grazing (DEKONINCK & BONTE, unpubl.). However, the cause of nest site translocation is still not understood (competition, parasitism, disturbance, ... – cf. GORDON, 1992 and SMALLWOOD & CULVER, 1979) and data on residence time of nests are often confusing: what exactly is a nest? *L. niger* for instance, has multiple nest sites with movements among them (see SMALLWOOD & CULVER (1979) and CULVER & BEATTIE (1980) for a brief discussion). The nest site turnover is different in different ant species and in different studies, suggesting both a species specific and a condition-related effect (presence of parasites, environmental conditions, etc.). There is no overall pattern. Mapping experiments using permanent quadrats and behavioural experiments (cafeteria experiments in the field and in the laboratory) could be useful in further research to help in understanding these complex interactions between ants, myrmecochores and external/internal factors influencing the turnover rate of nest sites.

As a conclusion, we can say that our results about spatial relationships between ant nests and myrmecochores are not in accordance with the results of OOSTERMEIJER (1989) in Terschelling. Whereas OOSTERMEIJER (1989) found a significant positive spatial relationship, this was not the case in the coastal dunes of Ter Yde (Oostduinkerke, Belgium): ant nests were not concentrated in plots where the myrmecochorous plants were abundant, nor

was there any special relationship within the plots. Slightly different habitat characteristics (in terms of infection rate by parasites, soil conditions, nest site turnover and availability of other food resources) could explain these different outcomes, taking into account both the chance for seedlings to establish on ant nests and the frequency of nest movements by ants.

## REFERENCES

- ALONSO, L.E. (2000). Ants as indicators of diversity. In: *Ants: Standard methods for measuring and monitoring biodiversity*. AGOSTI, D., J. MAJER, E. ALONSO & T. SCHULTZ (Eds.). Biological Diversity Handbook Series, Smithsonian Institution Press, Washington D.C. and London: 80-88.
- ASSING, V. (1986). Distribution, densities and activity patterns of the ants (Hymenoptera: Formicidae) of *Calluna* heathlands in northwestern Germany. *Entomol. Gen.*, 11 (3/4): 183-190.
- BLOMQUIST, M.M., H. OLFF, M.B. BLAAUW, T. BONGERS & W.H. VAN DER PUTTEN (2000). Interactions between above- and belowground biota: importance for small-scale vegetation mosaics in a grassland ecosystem. *Oikos*, 90: 582-598.
- BOER, P. (2001). Duinmieren en mierenduinen. *Duin*, 24 (4): 15-16.
- BOER, P. & T. DE GRUYTER (1999). *Mieren in de Noord-Hollandse duinen. Verspreidingsatlas. BOO-onderzoeksrapport*. Provinciaal Waterleidingbedrijf Noord-Holland, Bloemendaal (23 pp).
- BOND, W.J. & W.D. STOCK (1989). The costs of leaving home – Ants disperse myrmecochorous seeds to low nutrient sites. *Oecologia*, 81: 412-417.
- BOOMSMA, J.J. & A.J. VAN LOON (1982). Structure and diversity of ant communities in successive coastal dune valleys. *J. Anim. Ecol.*, 51: 957-974.
- BOOMSMA, J.J., A.A. MABELIS, M.G.M. VERBEEK & E.C. LOS (1987). Insular biogeography and distribution ecology of ants on the Frisian islands. *J. Biogeogr.*, 14 (1): 21-37.
- CULVER, D.C. & A.J. BEATTIE (1978). Myrmecochory in *Viola*: dynamics of seed-ant interactions in some West Virginia species. *J. Ecol.*, 66: 53-72.
- CULVER, D.C. & A.J. BEATTIE (1980). The fate of *Viola* seeds dispersed by ants. *Am. J. Bot.*, 67: 710-714.
- CULVER, D.C. & A.J. BEATTIE (1983). Effects of ant mounds on soil chemistry and vegetation patterns in a Colorado montane meadow. *Ecology*, 64: 485-492.
- DAVIDSON, D.W. & S.R. MORTON (1981). Competition for dispersal in ant-dispersed plants. *Science*, 213: 1259-1261.
- DEKONINCK, W. & D. BONTE (2002). Beïnvloeden mierennesten de verspreiding van planten in matig voedselrijke duinen? Resultaten uit Oostduinkerke. *Natuurfocus*, 1 (2): 61-64.
- GOMÉZ, C. & X. ESPADALER (1998a). Seed dispersal curve of a Mediterranean myrmecochore: influence of ant size and the distance to nests. *Ecol. Res.*, 13: 347-354.
- GOMEZ, C. & X. ESPADALER (1998b). Myrmecochorous dispersal distances: a world survey. *J. Biogeogr.*, 25: 573-580.
- GORB, S.N. & E.V. GORB (1998). Semenoj material moeravojnikov kak resoeht potoka semjan na territorijach *Formica polyctena* Fabr. vsjirokolistvennom lesoe=Seed pool of anthills as the result of seed flow on *Formica polyctena* Fabr. territories in a broadleaved forest. *Russian J. Ecol.*, 29 (1): 55-62.
- GORDON, D.M. (1992). Nest relocation in harvester ants. *Ann. Entomol. Soc. Am.*, 85(1): 44-47.
- GREEN, W.P., D.E. PETTRY & R.E. SWITZER (1998). Formicari-ous pedons, the initial effect of mound-building ants on soils. *Soil Survey Horizons*, 39 (2): 33-44.
- HANDEL, S.N. (1978). The competitive relationship of three woodland sedges and its bearing on the evolution of ant dispersal of *Carex pedunculata*. *Evolution*, 323: 151-163.
- HANDELMANN, D. (1997). *Dune insects-grasshoppers (Saltatoria) and ants (Formicidae). Coastal dunes. Management, protection and research*. Report from a European seminar, Skagen, Denmark (4 pp).
- HANZAWA, F.M., A.J. BEATTIE & A. HOLMES (1985). Dual function of the elaiosome of *Corydalis aurea* (Fumariaceae) – Attraction of dispersal agents and repulsion of *Peromyscus maniculatus*, a seed predator. *Am. J. Bot.*, 72 (11): 1707-1711.
- HIGASHI, S., S. TSUYAZAKI, M. OHARA & F. ITO (1989). Adaptive advantages of ant-dispersed seeds in the myrmecochorous plant *Trillium tschonoskii* (Liliaceae). *Oikos*, 54: 389-394.
- KJELLSSON, G. (1985). Seed fate in a population of *Carex pilulifera* L. 1. Seed dispersal and ant-seed mutualism. *Oecologia*, 67: 416-423.
- KOVÁR, P., M. KOVÁROVÁ, P. DOSTAL & T. HERBEN (2001). Vegetation of ant-hills in a mountain grassland: effects of mound history and of dominant ant species. *Plant Ecol.*, 156: 215-227.
- LACK, A.J. & O. KAY (1987). Genetic structure, gene flow and reproductive ecology in sand-dune populations of *Polygala vulgaris*. *J. Ecol.*, 75: 259-276.
- LISCI, M., M. BIANCHINI & E. PACINI (1996). Structure and function of the elaiosome in some angiosperm species. *Flora*, 191 (2): 131-141.
- LÓPEZ, F., F.J. ACOSTA & J.M. SERRANO (2000). Asymmetric interactions between plants and seed-harvesting ants in a Mediterranean pasture. *Ecol. Res.*, 15: 449-452.
- MCCUNE, B. & M.J. MEFFORD (1997). *Multivariate analysis of ecological data*. Gleneden Beach, Oregon: MjM Software.
- MULL, J.F. & J.A. MACMAHON (1997). Spatial variation in rates of seed removal by harvester ants (*Pogonomyrmex occidentalis*) in a shrub-steppe ecosystem. *Am. Midl. Nat.*, 138: 1-13.
- O'DOWD, D.J. & M.E. HAY (1980). Mutualism between harvester ants and a desert ephemeral: escape from rodents. *Ecology*, 61: 531-540.
- OHARA, M. & S. HIGASHI (1987). Interference by ground beetles with the dispersal by ants of seeds of *Trillium* species (Liliaceae). *J. Ecol.*, 75: 1091-1098.
- OHKAWARA, K., S. HIGASHI & M. OHARA (1996). Effects of ants, ground beetles and the seed-fall patterns on myrmecochory of *Erythronium japonicum* Decne (Liliaceae). *Oecologia*, 106: 500-506.
- OOSTERMEIJER, J.G.B. (1989). Myrmecochory in *Polygala vulgaris* L., *Luzula campestris* (L.) DC. and *Viola curtisii* Forster in a Dutch dune area. *Oecologia*, 78: 302-311.
- PROVOOST, S., C. AMPE, D. BONTE, E. COSYNS & M. HOFFMANN (2002). Ecology, management and monitoring of dune grasslands in Flanders, Belgium. In: *Littoral 2002. The Changing Coast*. EUROCOAST (Ed.). Eurocoast/EUCC, Porto: 11-22.
- RICE, B. & M. WESTOBY (1986). Evidence against the hypothesis that ant-dispersed seeds reach nutrient-enriched microsites. *Ecology*, 67: 1270-1274.
- SEIFERT, B. (1988a). A taxonomic revision of the *Myrmica* species of Europe, Asia minor, and Caucasica (Hymenoptera, Formicidae). *Abh. Ber. Naturkundemu.*, 62(3): 1-75.
- SEIFERT, B. (1988b). A Revision of the European Species of the Ant Genus *Chthonolasius* (Insecta, Hymenoptera, Formicidae). *Ent. Abh. Mus. Tierk. Dr.*, 51(8): 143-180.
- SEIFERT, B. (1996). *Ameisen, beobachten, bestimmen*. Naturbuch verlag, Augsburg and Berlin (352pp).
- SEIFERT, B. (1997). *Formica lusatica* n. sp. – a sympatric sibling species of *Formica cunicularia* and *Formica rufibarbis*



- (Hymenoptera, Formicidae). *Abh. Ber. Naturkundemu.*, 69(5) : 3-16.
- SERNANDER, R. (1906). *Entwurf einer Monographie der Europäischen Myrmekochoren*. Kungliga Svenska Vetenskapsakademiens Handlingar. Band 41.N17, 41/7 (410 pp).
- SERRANO, J.M., F.J. ACOSTA & F. LOPEZ. (1993). Belowground space occupation and partitioning in an ant community during succession. *Eur. J. Entomol.*, 90 : 149-158.
- SIEGEL, S. (1956). *Nonparametric statistics for the behavioral sciences*. McGraw-Hill Book Company Inc., New York-Toronto-London (312 pp).
- SMALLWOOD, J. & D.C. CULVER (1979). Colony movements of some North American ants. *J. Anim. Ecol.*, 48 : 373-382.
- SOKAL, R.R. & F.J. ROHLF (1981). *Biometry : the principles and practice of statistics in biological research*. 2nd edition. Freeman, San Francisco (859 pp).
- STATSOFT (1994). *Statistica for Windows*. Tulsa : OK. Statsoft, Inc.
- VAN BOVEN, J.K.A. & A.A. MABELIS (1986). *De mierenfauna van de Benelux (Hymenoptera : Formicidae)*. Wetenschappelijke mededelingen van de KNNV 173 (64 pp).